AGGREGATIONS OF MALE SCREWWORM FLIES, COCHLIOMYIA HOMINIVORAX (COQUEREL) IN SOUTH TEXAS (DIPTERA: CALLIPHORIDAE)

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Abstract.—Noted, for the first time, is the occurrence of aggregations of males of the screwworm fly, *Cochliomyia hominivorax* (Coquerel). The continuous presence of males in each of two sites in south Texas was independent of the presence of cattle or of female screwworm flies. Males captured in autumn 1975 proved to be wild; those captured in spring 1976 were released, sterile insects. The behavior of males, wild or sterile, included vigorous conspecific and interspecific interactions. There was evidence of territoriality and competition for favored perching sites. The observations are consistent with an hypothesis that the male screwworm aggregations were mating assemblies similar to those known among other cyclorrhaphan Diptera. The significance of male aggregation to sterile fly liberations is discussed.

Sterile fly release strategy, as currently practiced in the USDA, Southwestern Screwworm Eradication Program, is predicated upon three factors. One is that sterile Cochliomyia hominivorax (Coquerel) must be applied to areas where breeding may be occurring because the probabilities of detecting cases of myiasis, particularly when prevalence is low, are rather poor. Another factor upon which sterile fly dispersions is based is that of scale: Vast areas are at risk to primary screwworm and while it is possible to learn where breeding occurs, it is much more difficult to know where it is not. Thus great effort must be put to distributing sterile flies in areas that indeed have no screwworms at all. For these reasons, program aircraft are scheduled to "grid" evenly the region at risk. Generally, an area is treated to sterile flies packaged in units of 1,800-2,200 (1/2 males) and distributed in lanes set 5 or 10 miles (8-16 km) apart,1 "doses" of sterile flies varying with their availability and with case incidence reports submitted by ranchers, state, and federal personnel. The third consideration underlying sterile fly release strategy is the implicit assumption² that mating takes place after random dispersion of virgin flies from their pupation sites, a behavioral trait assumed to have evolved in order to prevent brothersister matings and consequent inbreeding. This supposition justifies the practice of distributing sterile flies in parallel lanes and requires of males that they seek out mates up to several miles from the point of their release. That they have the ability and necessary behavioral traits necessary to accomplish this was never demonstrated. It is therefore of very practical importance that we learn the sequence of events leading to mating; failing

this, that at least the operational premise of dispersion prior to mating is tested against such evidence as exists or can reasonably be inferred from data on related calyptrate fly species.

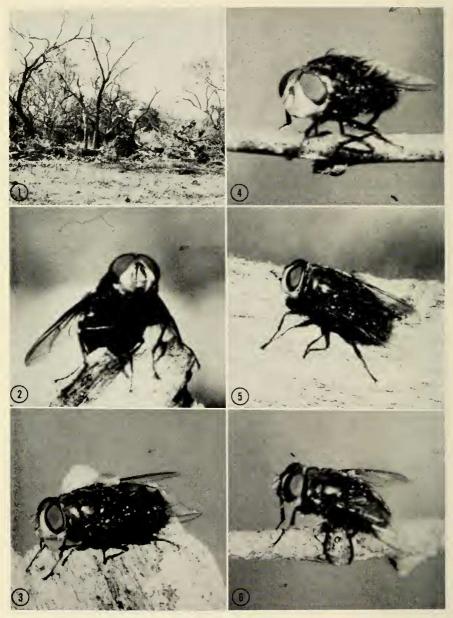
Observations

Two male screwworm aggregation sites, about 40 miles apart, were found in the thorny brush of northern Hidalgo County in south Texas. Male aggregation and mating behavior in screwworms has been heretofore unrecorded. The sites, wooded with Acacia spp. and mesquite (Prosopis spp.) up to about 7 m in height, were discovered in October 1975, and one of them (Fig. 1) was visited repeatedly until July 1976. Ladders were used when needed to gain access to perching sites. Where it proved impossible to get within a few feet of a specimen, identification was made through the use of a telescopic lens. Numerous color photographs were obtained. Discrimination of Cochliomyia hominivorax from C. macellaria (Fabricus) was easily accomplished visually. Captured material was used to confirm the identifications and some 16 crosses were made to laboratory-reared female C. hominivorax under controlled conditions (see below). Cochliomyia macellaria was commonly observed in the study locations, but males of this species were never observed to demonstrate the behavior characteristic of \hat{C} . hominivorax to be described, nor to occupy similar resting and perching sites.

Numbers of male *C. hominivorax* actually observed (simultaneously) varied from two to many on any one day, but their speed and frequency of flight were such that they proved impossible to census accurately. Even when three observers were present, simultaneous sighting of more than eight flies was difficult. More males than actually enumerated may well have been present. There was available no means which allowed us to make an unbiased estimate of male numbers, as the males moved rapidly through three dimensions and were not always easy to see. No screwworm males were observed in other locations similar to the identified aggregation sites nor were any found after repeated searching throughout the areas surrounding the two sites. Why these locations were preferred is unknown, as there seemed to be nothing particularly distinguished about them.

The aggregations of screwworm males were not dependent on the presence of livestock. When the present observations were begun, cattle were no longer to be found in site A, and only small, transient numbers of them were observed nearby in the year following. Site B was the home of a substantial herd of cattle, among whom were individuals infested with screwworms. Pens of wounded, sentinel sheep (Davis et al., 1968) were established in both aggregation sites. Gravid female *C. hominivorax* oviposit on the wounds and the resulting number of egg masses can be taken as an index of screwworm population density. No confusion exists between wild

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Figs. 1-6. Cochliomyia hominivorax, November 1975. 1. Aggregation site A. Trees are mesquite, *Prosopis*; 2-6. Male screwworms photographed in life, all on mesquite branches and twigs. Note that the flies face the sun.

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	Week beginning									Vari-
	10/22	10/29	11/5	11/12	11/19	11/26	12/3	12/10	Avg.	
Egg Mass Nos.										
Site A		1	13	1	0	1	0 —	0	2.3	22.6
Site B	5	18	24	9	0	0	0	0	7.0	87.7
Incidenceª	23	33	22	23	4	9	11	7	16.5	102.9
Avg. temps °C	21.7	23.5	23.3	18.3	13.4	15.4	17.3	18.9		

Table 1. Weekly screwworm egg masses, mean temperatures, and reported incidence of myiasis in Hidalgo County, Texas, 1975.

^a Based on samples of larvae voluntarily submitted by ranchers to the Southwestern Screwworm Eradication Program, APHIS, USDA.

and released, irradiated females because ovarian development does not occur in radiosterilized flies. Of 72 egg masses collected (Table 1), only four were sterile (6%), suggesting that sterile male releases of about 1,540 km²/ week were ineffective. The number of ovipositions were few in the first week of sampling, were greatest in the second or third weeks and declined precipitously thereafter. Screwworm incidence in Hidalgo County, as indicated by samples of larvae submitted to APHIS for identification, fell off less sharply than the local populations sampled in sites A and B. It is important to note that temperatures (Table 1) were adequate to allow ovarian development and do not explain the virtual cessation of oviposition. The egg-mass-sampling distributions were strongly clumped, as suggested by high variance to mean ratios. These are typical of screwworm populations in Texas and Mexico (Krafsur and Hightower, unpublished). The absence (in site A) or presence (in site B) of cattle seemed to have little influence on female screwworm populations.

Males continued to be seen until early December, well after the apparent dispersion of female screwworms. Three captured males were each caged with five virgin, laboratory-reared females. That the flies were wild was confirmed because only fertile egg masses were obtained. One of the males was caught in site B while feeding on a fresh cow dropping.

No evidence of screwworms was obtained after the advent of cold weather in December. Despite the continuous presence of wounded sheep in site A, no egg masses were found until 26 April, but male screwworms were observed from 5 March onwards. Some 13 were caught over a 3month period, and their fertility was tested by crossing them to laboratory-reared stock. All proved to be sterile, released flies. Females caught probing in wounds of the sentinel sheep also proved to be released flies, their ovaries failing to show evidence of yolk deposition after being held four days at 29°C. No male screwworms were observed on the sentinels, nor in their pens. Both sexes of *C. macellaria*, however, were frequent on sheep wounds and droppings. Nectar feeding among spring populations of screwworm males was suggested by the observation of heavy pollen deposits on some perching specimens.

Clear behavioral patterns were noted, and these were common to autumn, spring, and summer screwworm populations, being observed whenever the sites were visited, from 1000-1830 h. Resting males most frequently chose as perching sites prominent, leafless branches 3-6 m above ground level and facing open, sunny spaces. Distal perches were favored, but when these were occupied, exposed interstitial positions were assumed. Some male screwworms perched in leaves of the evergreen shrub, granjeno (Acanthoceltus spp.). Perching could easily be induced by holding up a stick or one's hand near a flight station or in one of the open "arenas." The new station usually would be taken by a nearby male. Characteristic, aggressive poses were adopted by perching males, heads up and abdomens down (Figs. 2-6). Cochliomyia macellaria were never seen to adopt such attitudes. When temperatures were about 20°C or higher, perching males periodically took off on short elliptical or circular flights; they quickly returned to the same positions unless displaced by another male. Vigorous interactions among screwworm flies were evident. A male occupying one site would reconnoiter other sites, and if occupied, interception and apparent conflict invariably occurred with two males flying off together in a mass of legs and wings, only to return to their respective stations. A perching male typically flew after screwworms, other fly species and even butterflies when these came within about 3 m of its resting position. Small numbers of perching sarcophagid and muscid males were occasionally noted.

On cool days, <20 °C, perching behavior was less frequently observed, and males could more easily be found resting closely appressed to the internodes of mesquite branches and twigs, usually exposed to the sun. This resting behavior supports the observations of Hightower (1963), who recorded nocturnal resting sites of marked, released screwworms. When windy conditions prevailed in addition, flies were found resting on mesquite twigs, within 1 m of the ground and *C. macellaria* were observed to behave similarly at such times.

Discussion

Observations made simultaneously on male and gravid female screwworm flies are consistent with an hypothesis that local aggregation of a cohort of females is transitory, while that of males is not. In other Diptera, males taken from a swarm or waiting station were demonstrated to return to their aggregation sites (Downes, 1969; Hunter and Webster, 1973). The sequence of events for most female screwworms seems to be, eclosion, mating at 2–3 days of age, oviposition at 5–6 days (Hightower et al., 1972) (should suitable hosts locally exist) and dispersion. This interpretation is supported by the clumped distribution of ovipositions observed in this and unpublished work conducted in Texas and Mexico. The sampling distribution of egg masses, typically aggregated spatially and temporally, probably arises from a similar distribution of larvae in their vertebrate hosts a generation earlier. Random dispersion before mating is the alternative. The hypothesis is unlikely. Recapture of sterile females is maximal on the third or fourth day after release, when the flies are 4-5 days old and already mated (Hightower, 1969). Cochliomyia hominivorax exist in characteristically low but highly aggregated density for much of their breeding season and over much of their range. The probability of encounter between the sexes of randomly dispersed screwworms, in the absence of a specific, long-range mechanism of attraction, must surely be very low. No such mechanism has been demonstrated, to my knowledge, among the Diptera. The principal cue initiating sexual activity, in many Diptera, is movement. Pheromones enabling sexual recognition over very short distances or upon contact have been demonstrated in the house fly and in a tsetse fly (Langley et al., 1975).

Male aggregations seem an altogether common phenomenon in many species of calyptrate flies, and are held to function as mating assemblies (see Downes, 1969 for review). The characteristic poses, territoriality, short, frequent flights among screwworms and their interactions with other flies differ little from that described for *Gasterophilus* sp. (Walton, 1930), the face fly, *Musca autumnalis* DeGeer (Teskey, 1969), several species of Cuterebridae (Catts, 1967; Hunter and Webster, 1973), *Oestromyia* sp. (Grunin, 1958), *Sarcophaga* sp. (Thomas, 1950), three species of Tachinidae and an anthomyiid fly (Lederhouse et al., 1976). Species of Syrphidae, Tabanidae, Tachinidae, Sarcophagidae, Calliphoridae, Muscidae, and Larvaevoridae have been observed in localized aggregations by Chapman (1954) and by Dodge and Seago (1954).

The significance of the present observations to sterile fly release operations is clear. The efficiency of the sterile male release method will be enhanced by maximizing the chances of putting sterile screwworms into actual or potential breeding sites. Numerous mark, release, and recapture studies on sterilized screwworm flies have demonstrated the extraordinary dispersal potential of females (Hightower et al., 1965). There is, however, no evidence at all to support the contention that released males disperse in this way.

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Footnotes

¹ This practice was discontinued in early 1977. Small fly containers and narrow swaths (~ 2 km) are now used. (See Krafsur, E. S., and L. Garcia. 1977. J. Med. Entomol. 14(6):687–697.)

² Made explicit by Bushland, R. C. 1975. Bull. Entomol. Soc. Am. 21:23-26.